

GENERAL NOTES

Autumnal Zugunruhe and migratory fattening of Dark-eyed Juncos apparently suppressed by detention at the wintering site.—Study of Zugunruhe, as a basis for determining the existence and intensity of the underlying physiological state of migrants, has established the importance both of internal factors such as circannual rhythms and of external environmental factors such as photoperiod in inducing and suppressing the migratory condition (Gwinner, pp. 391–410 in Aschoff, *Biological Rhythms*, Plenum Press, New York, New York, 1981). Other external factors that have been investigated are characteristics of the migratory destination (Wagner and Schildmacher, *Vogelzug* 8:18–19, 1937; Sauer and Sauer, *Vogelwarte* 20:4–31, 1959; Gwinner, *J. Orn.* 109:70–95, 1968; Gwinner and Czeschlik, *Oikos* 30:364–372, 1978). Transport of individuals in autumn to the winter range of the species (Gwinner 1968) or in spring to the breeding range (Emlen, *Auk* 84:309–342, 1967) has not suppressed Zugunruhe, nor has exposure of newly arrived migrants captured at their own individual destinations and held there had that effect in spring (Merkel, *Z. Tierpsychol.* 13: 278–301, 1956; Gwinner and Czeschlik 1978). However, interpretation of spring experiments is difficult because physiological changes associated with reproduction may be involved in terminating the vernal migratory state (Gwinner and Czeschlik 1978).

We asked whether detaining migratory Dark-eyed Juncos (*Junco hyemalis hyemalis*) outdoors during the breeding season at a location in which they had wintered in previous years would inhibit normal Zugunruhe and migratory fattening the following autumn. This detention (at Bloomington, Monroe Co., Indiana, 39°N, 87°W) exposed the birds in the weeks preceding the normal migration season to the environment of the precise location to which they would have migrated, had they summered on their northern breeding range. If the birds recognized the site as their goal, possibly their migratory physiology would be affected, although the absence of effect would not necessarily indicate non-recognition. Our findings suggest that characteristics of the migratory destination can terminate, or perhaps even prevent initiation of, the migratory state, at least in autumn.

The migratory eastern junco.—Migratory members of *J. h. hyemalis* in eastern North America move between a summer range located largely in Canada and a winter range covering nearly the entire eastern United States. Fall migrants probably begin to leave the breeding range in August, and winter populations build up until about 1 December, when migration ceases (Ketterson and Nolan, *Ecology* 57:679–693, 1976). Probably throughout the winter range, spring migration begins about 1 March; some juncos are found in the northern reaches of the winter range until mid-May. Sex and age classes differ in distance migrated: females travel farther than males, on the average, and adults tend to winter south of young hatched during the preceding breeding season (Ketterson and Nolan 1976; *Auk* 96:532–536, 1979; *Auk* 99:243–259, 1982; *Current Ornith.* 1:357–402, 1983).

Adult male juncos are faithful to their previous breeding sites, adult females less so (Ketterson and Nolan 1983; pers. obs.). Our investigations of winter populations at five latitudes (33°N–42°N) have shown that some males and females return every winter to the same few hectares (Ketterson and Nolan 1982). Once it has shown site fidelity, a junco probably returns to that site every winter until it dies; we base this conclusion on high annual rates of return (53%) after the first expression of winter site fidelity (Ketterson and Nolan 1982). Thus, a junco that in the future would be faithful to its winter site can be identified by its having returned in the winter following that in which it was banded.

Juncos hatched during the preceding breeding season can be aged until about 31 December by inspection of skull pneumatization. Birds in their second winter cannot be distinguished

from older birds. Determination of sex by external characters is reliable (Ketterson and Nolan 1976).

Methods.—We divided juncos into three groups, which differed in their previous histories but not in experimental treatment. Experiments were done in autumn 1980 and spring 1981. Except during experiments, groups were intermingled in large outdoor cages (e.g., about $7 \times 4 \times 3$ m). Group histories before the experiments were as follows.

Group I (two males and two females): All had wintered at least twice at Bloomington before the experiment. Three were banded during the winter of 1978–79 and immediately released; the fourth was banded in 1976, released, and caught again at the same place in the following winters. All were captured in 1979–80 at their original capture sites, three near the aviary cages in which we subsequently held them and the fourth 1.5 km from the aviary. Thus, from last recapture until the experiment began in September 1980, at least three of the four could see surroundings long familiar to them. The breeding locations of Group I birds were unknown.

Group II (one male and one female): The female, adult when caught on 1 August 1979 at Timmins, Cochrane Co., Ontario, Canada (49°N , 81°W), and the male, immature when caught on 3 September 1979 at Wawa, Algoma Co., Ontario (49°N , 85°W), were transported within 2–3 days approximately 1250 km southward to Bloomington and caged. Therefore, Group II was like Group I in that its members had no experience on the breeding range during the spring and summer preceding the autumn experiment. Group II differed from Group I in that the Group II birds had been transported into the winter range instead of having been caught there; the immature male had never migrated and had never been on the breeding grounds as an adult. Probably the most important difference between Group I and Group II members is that the sites to which Group II would have migrated in autumn were unknown. The probability that Group II juncos would have settled at or even passed through Bloomington is negligible given the extensive winter range of migratory juncos.

Group III (eight males and eight females in the autumn experiment, three of the same males and six of the same females in the spring experiment): We caught these as breeding adults in late July 1980 at Wawa, took them immediately to Bloomington, and caged them with the other groups. All could have been as old as or older than the members of Group I and Group II, and some probably were (see below). All had spent at least one winter living free before capture; and, as with Group II, very likely none had ever wintered at or passed through Bloomington.

On 3 September, members of groups were randomly assigned to individual steel-wire cages ($21 \times 27 \times 20$ cm) on the roof of a five-story building 1.5 km from the outdoor aviary. The birds were visually isolated but could hear each other. Transparent plexiglass covers sheltered cages from rain, and during severe precipitation larger sheets of plywood were set on top of the plexiglass. All birds could see a segment of sky whose north–south angle was about 160° and whose east–west angle was about 100° . The segment seen varied slightly from cage to cage, and most birds were moved occasionally from one cage to another. We observed no changes in behavior or physical condition as a result of shifting birds to different cages.

Dim light reached the roof from windows of a building about 100 m distant, but the juncos could not see these windows. A calibrated Tektronix J6511 photometer with its illuminance probe directed upward from the roof floor at the midpoint of the layout of cages recorded lux values (\bar{x} of five readings) of 0.050 on cloudy nights, 0.229 on half-moonlit nights, and 0.267 on full-moonlit nights.

The geomagnetic fields within the aviary cages differed little or not at all from the normal local field; but from one experimental (registration) cage to another the horizontal angle of a compass needle varied by as much as 100° , apparently because of variation in the proximity

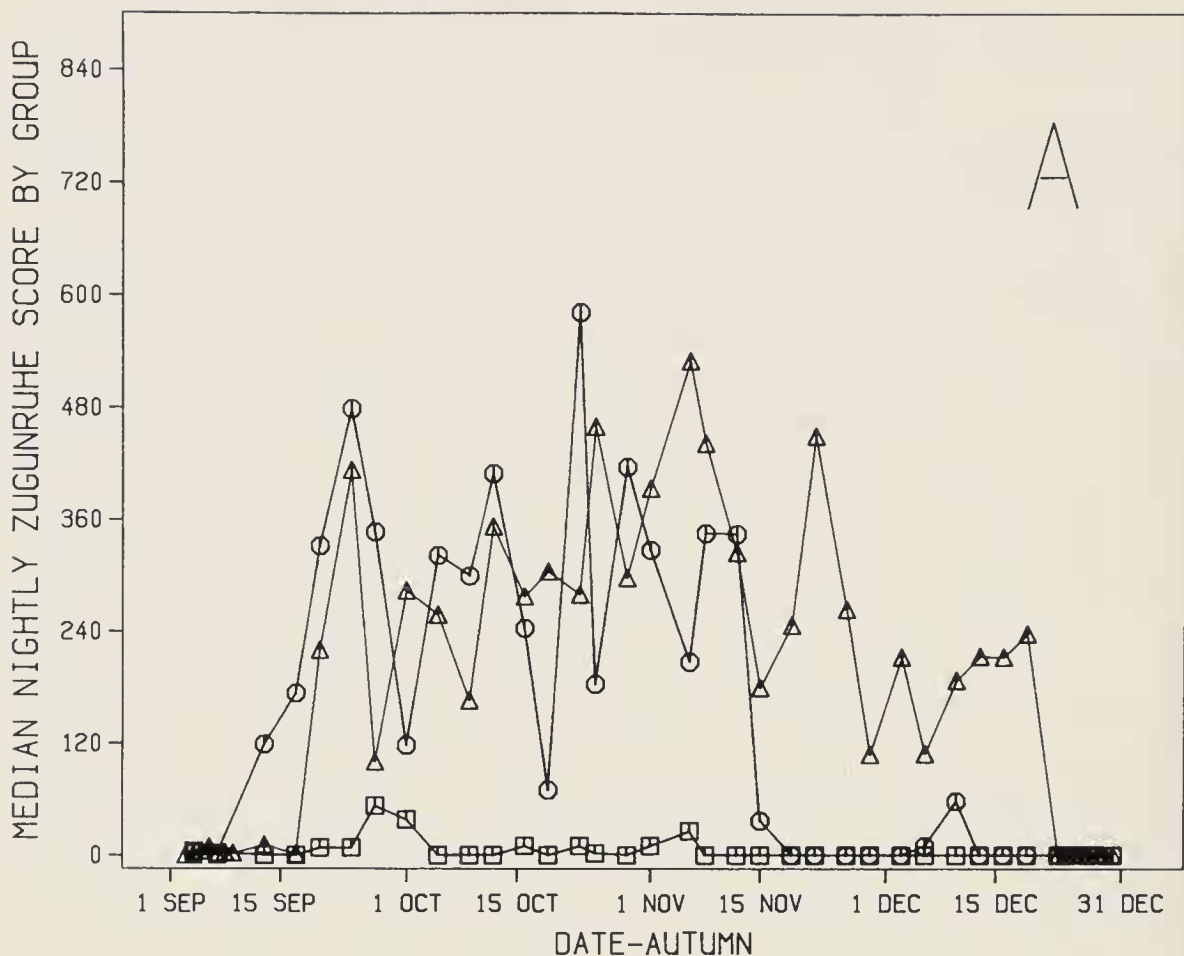
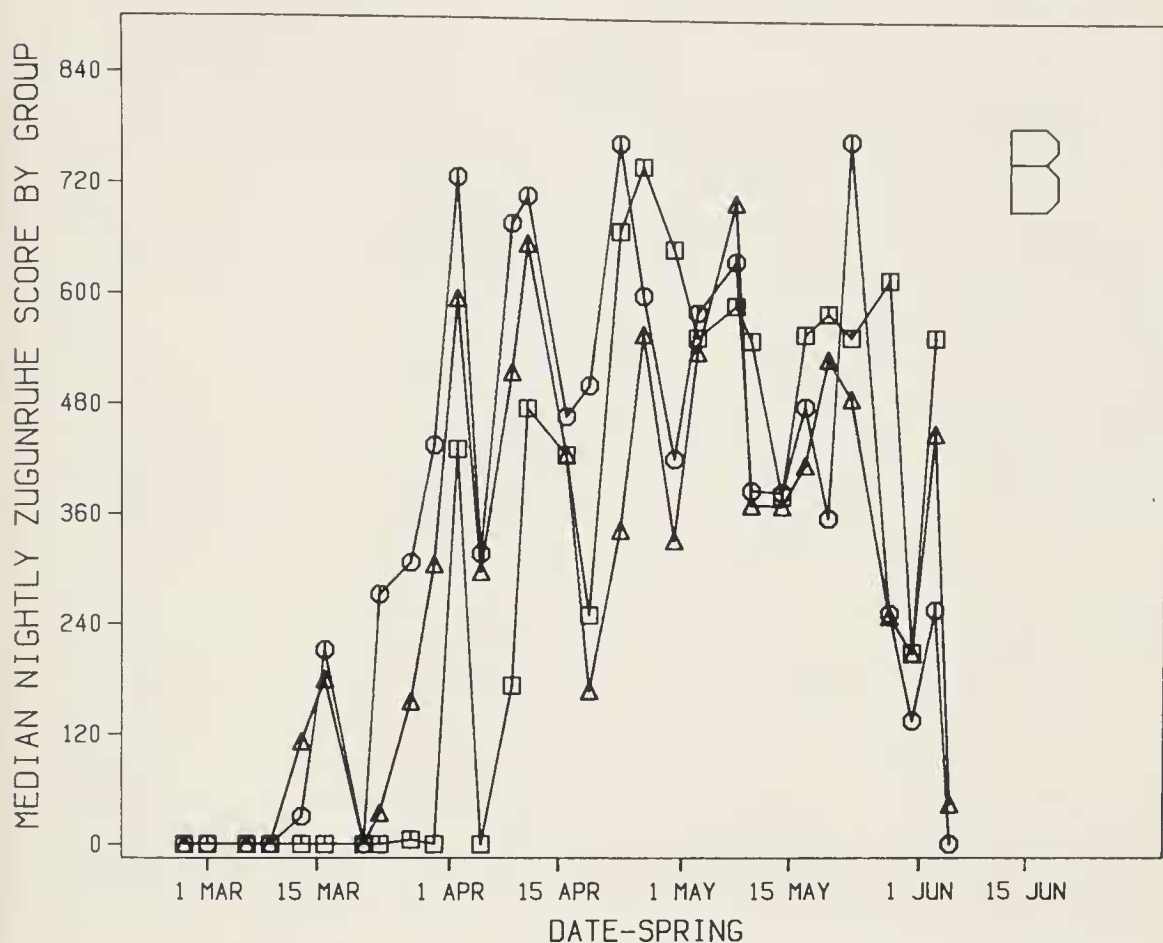


FIG. 1. (A) Median nightly Zugunruhe scores of three groups of Dark-eyed Juncos on 2 nights per week in autumn 1980. See text for methods. Square symbols indicate Group I, circles Group II, triangles Group III. (B) The same, spring 1981.

of girders and a nearby machine room and, perhaps, differences in remnant magnetism among the cages.

Each cage's perch was attached to a microswitch connected to an Esterline-Angus event recorder. Every use of the perch was recorded on a strip chart moving at 30.5 cm/h. We tallied 30-sec intervals during which a cage's perch was activated at least once and then counted the number of such intervals among the 900, 30-sec intervals that fall between 21:00 and 04:30. We selected these hours because they encompassed the period of darkness on the longest days of both autumn and spring. The number of an individual's active 30-sec intervals is its nightly Zugunruhe "score." We found for each individual its seasonal score (sum of nightly scores), maximum nightly score, and number of nights it was active for at least 30 min (i.e., nightly score ≥ 60). We also computed medians of the nightly scores according to group.

Compilation of all nightly scores in autumn 1980 revealed that scores from two nights per week were sufficient for the purposes of this paper. Therefore, we analyzed and present data from only two nights per week in both the autumn and spring experiments; single scored nights were separated by two, three, two, three, etc., unscored nights. A total of 33 nights were scored in the autumn experiment (7 September–26 December), 28 nights in the spring experiment (26 February–31 May).



Because the sexes were equally represented in each autumn group, we have simplified the presentation by pooling results from the sexes. Occasional gaps in the nightly record for individual cages were caused by equipment failures and by exercise periods (see below). To reduce the effect of these on total seasonal scores, we arbitrarily assigned to a missing score the mean of the individual's score on the two nights preceding and two nights following the gap. In spring 1981, a Group I female escaped when five scoring nights remained before the experiment ended. Because Group I was small, data for this female are nevertheless used and are presented without extrapolating to scores for the missing nights.

Four birds at a time were taken separately in opaque bags to exercise in the outdoor aviary for 2 or 3 days in early or mid-November. There the large cages were divided into individual compartments (about $3.5 \times 2.0 \times 3.0$ m), each covered by cloth so that its occupant could see no other experimental bird but could see the sky and surroundings in two directions. In spring 1981 there was no interruption for exercise.

Weights (to 0.1 g on a 50-g Pesola balance) and subcutaneous fat classes (0-5 with zero low, as described by Helms and Drury [Bird-Banding 31:1-40, 1960], and Nolan and Ketterson [Wilson Bull. 95:603-620, 1983]) were determined in mid-afternoon at the beginning and end of both experiments and also at approximately 2-week intervals during experiments. Autumn weights are analyzed only for the values recorded through 1 December because the tendency of juncos to fatten in winter could confound interpretation of December weights. (In fact, December weight changes were small or absent.) Male juncos average larger than females. However, because we present means of absolute individual gains and of gains as a percentage

TABLE 1
ZUGUNRUHE SCORES^a IN AUTUMN 1980 AND SPRING 1981, ACCORDING TO GROUP

Season and group	Seasonal score	Median (extremes) ranks ^b	
		Maximum nightly score	Nights scored >60
Autumn			
Group I	310 (187, 1137) 1, 2, 3, 5	122 (55, 465) 1, 2, 3, 7	2 (0, 4) 1, 2, 3, 4
Group II	5502 (3760, 14,243) 7, 15	598 (508, 688) 9, 17	17.5 (17, 18) 6.5, 8
Group III	6511 (1023, 13,366) all others	604 (247, 828) all others	22.5 (6, 29) all others
Spring			
Group I	7840 (2533, 12,478) 2, 6, 7, 15	753 (567, 877) 2, 3.5, 9, 15	14 (8, 17) 1, 4.5, 4.5
Group II	10,054 (9500, 10,609) 10, 12	804 (778, 830) 8, 13	20 (18, 22) 6, 12
Group III	9113 (1705, 11,926) all others	766 (230, 837) all others	20 (9, 24) all others

^a See text for methods.

^b The number of juncos ranked was 22 in autumn, 15 in spring.

of initial weight, for each group we pooled data without regard to sex. Increases in weight were accompanied by increases in fat class, and we believe that the weight gains observed were largely the result of fattening (see Nolan and Ketterson [1983], for the correspondence between winter weights and fat class).

Results.—In the autumn experiment the birds of Group I were much less restless than were members of the other two groups, which among themselves were indistinguishable in their Zugunruhe. Fig. 1A shows the nightly medians of each group and reveals how greatly Group I differed from the others in this respect. Table 1 presents for each group its median score and the lowest and highest score of its members for the three measures of Zugunruhe. It also gives, for each measure, the ranks of the scores of group members when all 22 birds were pooled and ranked, lowest to highest. In a Mann-Whitney *U*-test, Groups II and III did not differ in any measure. For seasonal score, $U = 11$, 2-tailed $P > 0.10$; for maximum nightly score, $U = 13$, 2-tailed $P > 0.10$; for nights scored above 60, $U = 13$, 2-tailed $P > 0.10$. Accordingly, we pooled Groups II and III and tested them against Group I. For seasonal score, $U = 1$, 2-tailed $P < 0.002$; for maximum nightly score, $U = 3$, 2-tailed $P < 0.002$; for nights scored above 60, $U = 0$, 2-tailed $P < 0.002$.

Mean autumn weight gain by members of each group is shown in Table 2. Group I birds gained much less than did members of the other two groups, which did not differ among themselves. As in Zugunruhe, Groups II and III were combined because they were similar (absolute gain, $U = 15.5$, 2-tailed $P > 0.10$; percentage gain, $U = 13$, 2-tailed $P > 0.10$). Group I differed significantly from Groups II–III (absolute gain, $U = 4.5$, 2-tailed $P < 0.02$; percentage gain, $U = 6$, 2-tailed $P < 0.02$). Fat classes at time of maximum weight for Group

TABLE 2
WEIGHT GAINS^a IN AUTUMN 1980 AND SPRING 1981, ACCORDING TO GROUP

Season and group	Mean (extremes) ranks ^b	
	Absolute gain (g)	Gain as % of initial weight ^c
Autumn		
Group I	2.15 (0.5, 2.9)	12.0 (0, 18)
	1, 3, 4.5, 6.5	1, 3, 5, 7
Group II	4.90 (4.0, 5.8)	24.5 (21, 28)
	9.5, 16	10, 14
Group III	5.14 (2.0, 8.5)	28.6 (10, 52)
	all others	all others
Spring		
Group I	6.00 (5.1, 6.8)	32.9 (29, 35)
	8, 9, 11, 13	9, 11, 12, 14
Group II	6.35 (6.0, 6.7)	29.0 (25, 33)
	11, 12	8, 10
Group III	3.98 (1.1, 7.1)	20.8 (6, 47)
	all others	all others

^a In autumn, means of initial and of maximum absolute weights (g) by sex for each group were: for Group I males 18.8, 20.6, for females 17.5, 20.0; for the Group II male 18.8, 22.8, for the female 20.7, 26.5; for Group III males 19.4, 24.0, for females 17.1, 22.8. In spring, means of initial and maximum absolute weights (g) by sex for each group were: for Group I males 18.3, 24.6, for females 18.0, 23.6; for the Group II male 20.3, 27.0, for the female 23.9, 29.9; for Group III males 21.1, 25.0, for females 18.6, 21.9.

^b The number of juncos ranked was 22 in autumn, 15 in spring.

^c The percentage gain of each individual was determined from its initial and maximum weights; percentages were summed within groups, and means per group were derived from sums.

1 birds were 0, 1, 1, 2. Only one of the Groups II–III juncos was classed as 1, and the median rank was 4.

In spring, Zugunruhe of all juncos was greater than in fall, and the intergroup differences that had existed in autumn disappeared (Fig. 1B and Table 1). As before, we compared Group I juncos to Groups II and III combined, using Mann-Whitney tests of ranks: for seasonal score, $U = 21$, 2-tailed $P > 0.10$; for maximum nightly score, $U = 17.5$, 2-tailed $P > 0.10$; for number of nights scored above 60, $U = 4$, 2-tailed $P > 0.05$. In this last comparison the female that escaped before the end of the experiment is excluded. The trend toward fewer nights with activity in Group I can be seen in Fig. 1B; Group I birds did not become active until about 1 April, when their Zugunruhe set in rather synchronously and thereafter remained high.

In spring weight and fattening, Group I birds became as heavy as, or heavier than, the other juncos (Table 2). For absolute gain and percentage gain, $U = 13$ and 8, respectively, 2-tailed $P > 0.05$. Fat classes at the time of maximum weight for Group I birds were 4, 4, 4, 5. Both Group II birds were classed as 5, and the median class of the Group III birds was 3.5.

Discussion.—Our samples were small, but we very cautiously suggest that the site-faithful juncos did not enter the normal autumn state because they were already at the place to which they would have migrated had they been free. Other factors that might have sup-

pressed the migratory state, but that we tentatively reject, are advanced age and long captivity, possibly coupled with group living, and/or exposure to a pre-migratory photoperiodic regime unlike that of the breeding range. Although older juncos sometimes show less autumn Zugunruhe than young of the year (Swanson, M.A. thesis, San Jose State Univ., San Jose, California, 1976), age seems to us an unlikely explanation for our results because at the time of the autumn experiment all members of each group would have been making at least their second autumn migration. Group I subjects would have been making at least their third; but given the junco's 53% annual survival rate (Ketterson and Nolan 1982, 1983), probably at least half the Group III subjects would have been doing the same. Captivity of Group I at Bloomington and the fact that they shared aviary cages with 15–20 other juncos at the time when Group III juncos were breeding could account for the difference between those two groups, but Group II was held with Group I and nevertheless fattened and grew restless. Group II subjects had, in fact, been held 4–6 months longer than Group I; yet in all measures of Zugunruhe both Group II members ranked higher than all Group I members (1-tailed $P = 0.067$, the lowest possible value for samples of two and four). Daylength during summer is considerably shorter at Bloomington than at Wawa (1 h 40 min shorter on the longest day). Recent work by Moore et al. (Condor 84:410–419, 1982) suggests that in White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) the normal expression of the autumnal phase of the annual cycle requires exposure to 16-h days. The longest day at Bloomington is 15 h 58 min, and this might have suppressed Zugunruhe and fattening in the Group I juncos. Here again, however, members of Group II also experienced these shorter days and despite that were more like Group III than like Group I.

If recognition of some feature(s) of the winter site did have the suggested effect, what might the feature(s) have been? The local geomagnetic field of Bloomington is a possibility. The birds were exposed to this force until the experiment began; thereafter, however, they experienced disturbed fields that varied from cage to cage. Visual cues characteristic of the latitude and longitude of the winter range have been thought (Wagner and Schildmacher 1937) to influence Zugunruhe. More specifically, Sauer and Sauer (1959) reported that sight of the starry African sky suppressed restlessness in members of four *Sylvia* species displaced to their winter quarters (and beyond) in Africa. An obvious difficulty with applying this suggestion to our Group I results is that the stars (except Polaris) at Bloomington in the weeks preceding the autumn experiment, i.e., in the period in which suppression of the migratory condition supposedly occurred, were in different positions from their positions in winter. Therefore, the juncos, if they looked at the stars, did not see the familiar sky of their winter site. A final familiar feature to which the Group I juncos were exposed was the landscape. Three individuals in at least two winters had home ranges around the aviary cages in which they spent the summer before the experiment. The fourth had been caught and recaptured 1.5 km distant, but nevertheless could have known the aviary grounds; occasionally banded individuals have moved back and forth between the aviary and the station where this fourth bird was caught.

The suggestion that familiar surroundings inhibited the migratory condition in Group I is not inconsistent with the notion that an endogenous circannual rhythm or that photoperiod regulates migration in juncos. Even in his early report of circannual rhythms in *Phylloscopus* spp., Gwinner (1968) emphasized that although displacement to the winter range of the species had not suppressed Zugunruhe, displacement to the individual's precise winter quarters might cause suppression. To relate our autumn experiment to Gwinner's, our Groups II and III roughly correspond in treatment and in results to his Group III; but our Group I had no counterpart in his experiment.

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Baxter welcomed us to Wawa and helped us catch juncos there. Judson Mead, Rod Suthers, and Gary Hafner lent us equipment to measure geomagnetism, Zugunruhe, and light intensity, and we thank them. Donald S. Farner kindly read and commented on an earlier version of the manuscript. This work was supported in part by NSF DEB-78-11982 and DEB-81-10457. We dedicate this paper to the memory of Cindy B. Patterson.—ELLEN D. KETTERSON AND VAL NOLAN JR., *Dept. Biology, Indiana Univ., Bloomington, Indiana 47405. Accepted 10 Aug. 1983.*

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Mimicry of the human voice by European Starlings: the role of social interaction.—Although vocal mimicry by European Starlings (*Sturnus vulgaris*) has often been noted (e.g., Bent, U.S. Natl. Mus. Bull. No. 197, 1950), the development of it has never been formally studied. The present report describes social constraints on starling mimicry and suggests possible functions. Although the targets of the mimicry here were humans, the major aim of the study was to understand how starlings naturally select sounds for mimicry. In other words, is their mimicry a faithful imitation of their social or physical surrounding or is it, as in most other species, quite biased toward a particular class of sounds? Because humans can detect speech more acutely than avian sounds, speech mimicry was used as an analogue to natural starling mimicry. As the presence of speech could be easily perceived, it would thus be possible to identify the origins of any mimicked sounds, as well as conditions under which starlings mimic their social world.

Methods and materials.—Seven starlings, four females and three males, were captured as five-day-old nestlings (Table 1). They were hand reared in the laboratory by the investigators until approximately 30 days of age. During this period, they were maintained as a group with equivalent and extensive contact with human caretakers. At day 30, a male and a female were assigned to the interactive contact (IC) condition, a male and female to the limited contact (LC) condition, and the remaining three to the auditory contact (AC) condition. IC1 and IC2 each remained in the homes of the respective investigator who had reared them. Each received daily vocal attention and companionship from its human caregiver. In addition, each had a male Brown-headed Cowbird (*Molothrus ater*) housed with it in a 0.7 × 1.3 × 1.3-m hardware-cloth cage. Explicit attempts to “teach” IC1 and IC2 speech were avoided, i.e., food or social contact was not offered as a reward for mimicry although each of these items was clearly sought by the birds. Whistled songs (e.g., “Dixie,” “Popeye the Sailor”) were performed daily, usually when the birds were allowed to fly free and interact with their human caregivers. Mimicry by IC1 and IC2 was often imitated by the humans but again only in an unsystematic manner, i.e., the humans did not consciously imitate sounds as a particular strategy. Finally, IC1 and IC2 were exposed to tape-recorded passages of human speech and whistled songs twice daily for one month.

The LC starlings were also housed in homes, but with different caregivers who had not participated in the starlings' care as nestlings. Each bird was also housed with a cowbird companion. Because these birds were less “tame” with their new human caregivers, they were rarely allowed to fly free or to contact humans directly. Each was housed, however, in a room allowing it extensive vocal stimulation from humans. That is, they heard speech in their environment but were not “spoken to” consistently or allowed interaction with humans. The LC birds were not tutored by tape recordings. The AC birds were housed as a group in a cage (4.8 × 4.8 × 3.2 m) on a screened porch belonging to one of the investigators where they could hear all of the interactions inside the home where IC2 was housed. As a result, the auditory environment of the AC birds was yoked to the IC condition. Thus, they were